PLANT AND BAT INTERACTIONS IN WEST AFRICA[1]

EDWARD S. AYENSU[2]

ABSTRACT

One of the most dramatic plant and animal relationships in the West African ecosystem is that which takes place between such frugivorus bats as *Epomophorus gambianus* and *Eidolon helvum* and the introduced neem tree, *Azadirachta indica*. While earlier studies on bat behavior were carried out by personal observation and ordinary photographic means, recently developed night vision equipment has allowed the author to make nocturnal observations previously not possible. New observations, using this equipment, have now been made on bats and their interaction with trees of the following species: *Mangifera indica, Anacardium occidentale, Ficus umbellata, Psidium guajava, Carica papaya, Kigelia africana, Spathodea campanulata, Parkia clappertoniana, Ceiba pentandra,* and *Adansonia digitata.* Observations are reported on the roosting characteristics of bats of the genus *Epomophorus*. The effect of feeding by bats on the fruits of various trees and the resulting dispersal of seeds on the coastal savannah-grassland, (Accra Plains) of Ghana, are discussed. The effect of introduced plants on the bat population and disadvantages to the West African ecosystem which are attributable to the plant and bat interactions are summarized.

Throughout the history of human societies bats have had an unchallenged notoriety in the realm of superstition and mythology. As the only known flying mammals, bats have for centuries been associated with various mysterious nocturnal activities. The Chinese are perhaps the only people who consider bats as objects of good luck and happiness. The Chinese word for bat is *fu* which signifies happiness (Allen, 1962). In many primitive societies bats have been associated with the dead, who are believed to possess souls that have the ability to fly freely at night when the living are asleep. In West Africa as well as in other regions of the world, several mythical stories about bats have been handed down from one generation to the next. Even today superstitious stories about bats are told to children. Bats are considered sinister, and their unexpected nightly visitations are believed to be signs of ill omen in some societies.

It is not unusual, therefore, that bats are looked upon from various perspectives in West Africa (Fig. 1). They are considered by many as animals with supernatural powers which should be avoided at all cost, especially at night because of their purported evil intentions. The West African Moslems, for example, place bats in the same category as pigs, because they are considered unclean; their peculiar roosting position is thought to make it easy for them to urinate on themselves. It should be noted that the Egyptians used sketches of bats as a symbol of a nursing mother, "for it is the only flying creature that has teeth and two nipples and nurtures its young with care" (Allen, 1962: 2). In southwest Ghana (Fig. 2) some of the people of Half Assini use the bat as the tribal totem. The clan therefore is forbidden to eat bats. Since bats often live near areas of

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[2] Department of Botany, Smithsonian Institution, Washington, D.C. 20560.

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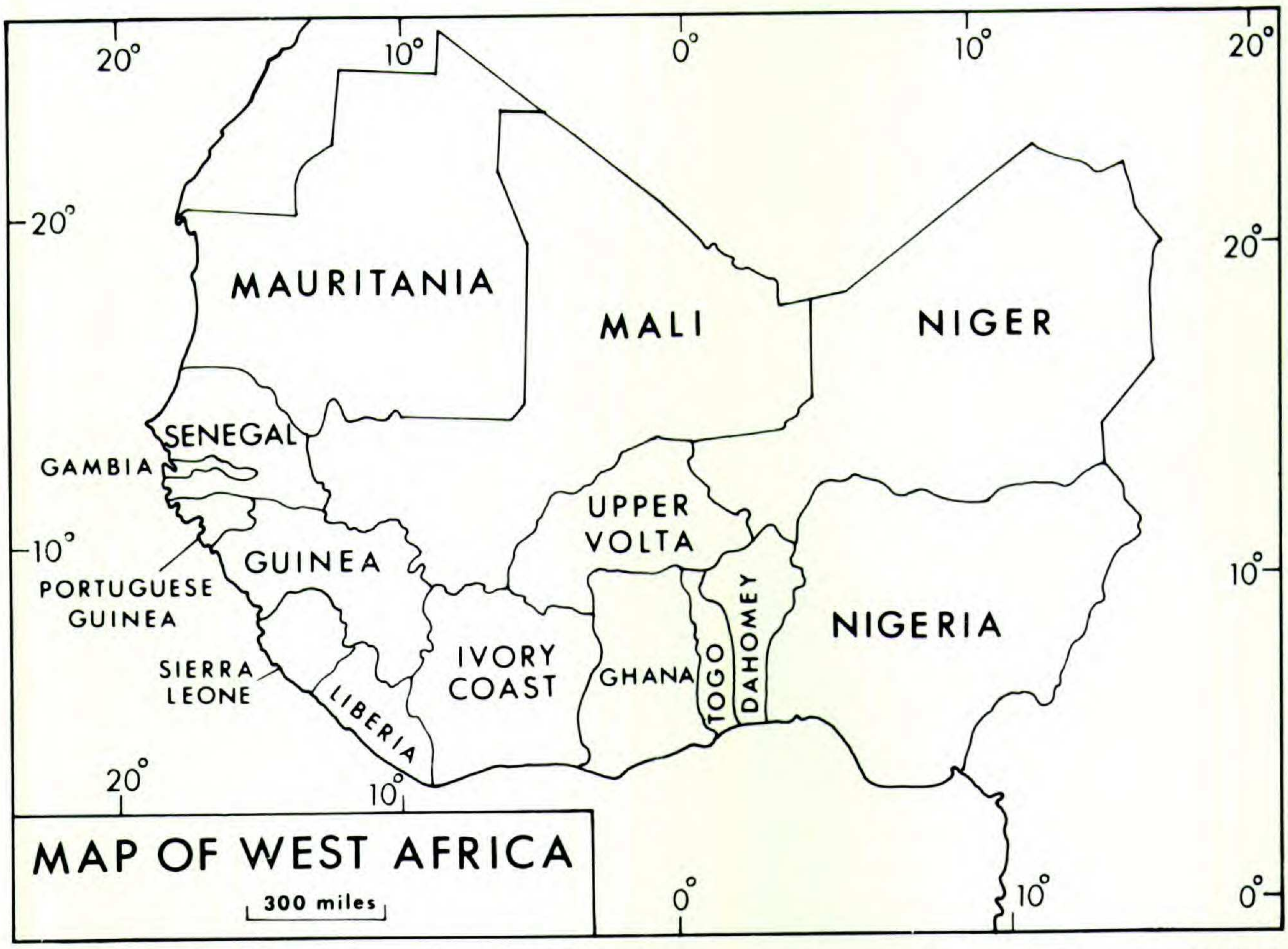


FIGURE 1. Political boundaries of West African countries where several genera of fruit bats occur.

human habitation, they are regarded as a public nuisance, because they roost on and in buildings and leave waste products on ceilings and in crevices. Bats are also considered destructive. In some areas fruits such as mangoes, guavas, and papayas are destroyed by bats during feeding. Besides their negative attributes these vegetarian bats (fruit bats) are a source of meat to some people in West Africa. In Ghana, for example, some of the Kwahus, the Ashantis, and the Brongs take bat meat as a significant source of protein in their diet apart from considering this meat a delicacy.

Several years ago I became acquainted with the fact that certain plants partly owed their continuous existence to the fact that their prinicipal pollinators were bats. Two plant biologists, Drs. Herbert G. Baker and B. J. Harris, were responsible for the renewed interest in the observation of the behavior of bats on plants in West Africa about the mid-1950's. Most of the studies of Baker and Harris were conducted in the vicinity of my high school (Achimota Secondary School) grounds. I was naturally familiar with the tree populations on which their studies were based, and I have since continued to observe the plant and bat interactions at the same site.

REVIEW OF PAST RESEARCH

The first description of bat visitation to flowers of the Baobab (*Adansonia digitata*) in Africa was by Jaeger (1943) in Senegal. But it was Baker and Harris who actually stimulated public awareness of pollination of flowers by bats in

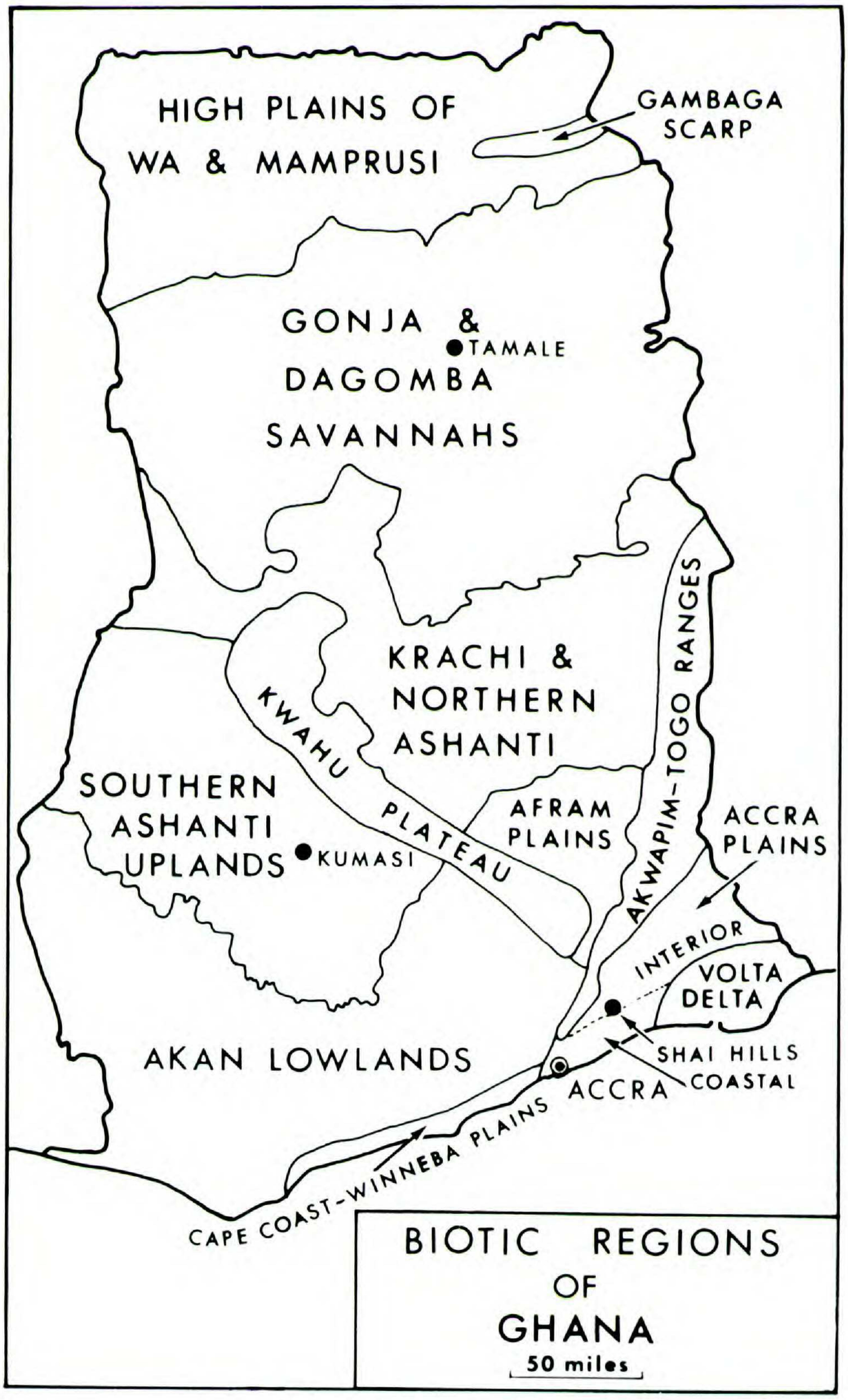


FIGURE 2. Biotic regions of Ghana.

this region. Their studies concerned four well known plants: *Parkia clappertoniana* (dawadawa), *Kigelia africana* (Sausage Tree), *Ceiba pentandra* (Silk-Cotton Tree or Kapok Tree), and *Adansonia digitata* (Baobab Tree).

Parkia clappertoniana is one of the characteristic tropical trees that loses its leaves during the dry season. In West Africa leaf fall in *Parkia* occurs from late October to early February. With the loss of leaves comes the production of red ball-like inflorescences, each containing about 2,000 flowers. The flowers are

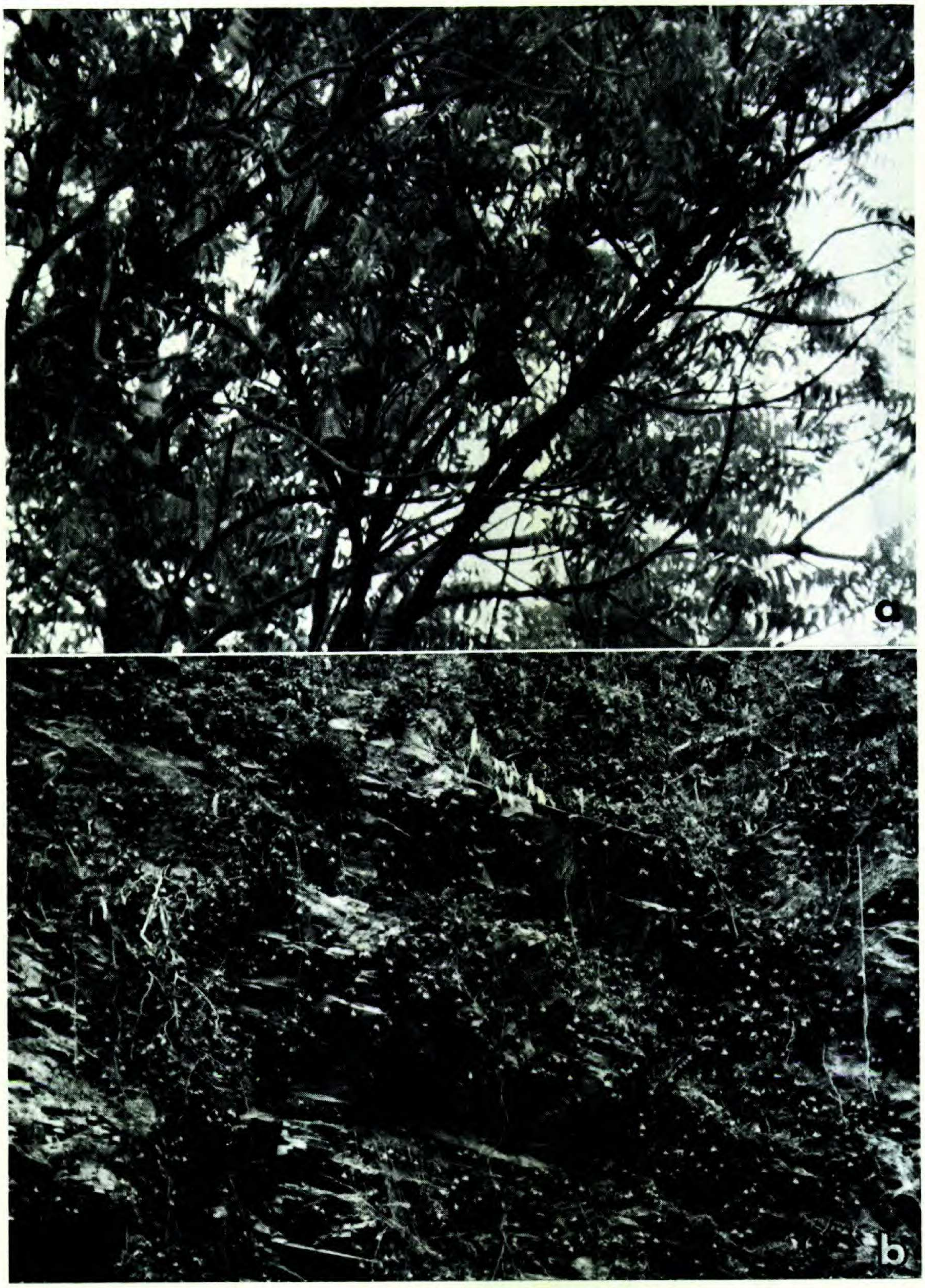


FIGURE 3.—a. A colony of Gambian Fruit Bats, *Epomophorus gambianus* roosting in *Azadirachta indica*.—b. Large numbers of *Epomops franqueti* roosting on the east face of the Lilidze Mountain Range.

protandrous, *i.e.* anthers ripen before the stigmas. Baker and Harris (1957) and Harris and Baker (1959) reported that when the flowers first open they are deep red with ripe anthers (male condition), but by the following day the flowers become pinkish as the stigma (female condition) protrudes. With the opening of the flower by late afternoon and just before dusk, the fruit bats begin to visit the flowers. Baker and Harris noted that the first bats to visit the *Parkia* flowers were *Epomophorus gambianus*. These bats visit the trees for about twenty minutes, more or less restricting their visit to the upper part of the tree. The bats generally insert their snouts into the depressions on the upper part of the florescence where nectar collects. They often lap the nectar continuously for periods of fifteen to forty-five seconds at a time. The gentle flapping of their wings helps to maintain their balance, while the fur on the head, especially on the underside of the jaw, the throat and on the chest, collects pollen which is later transferred to the stigma of other flowers. Other bats that were observed to make subsequent visits included *Nanonycteris* and *Eidolon*.

Studies of the visitation to *Kigelia africana* (Sausage Tree) shows that when the flowers open, Dwarf Epaulet fruit bats (*Micropteropus pussilus*) often land at the lower lip of the flower and insert their heads in the floral cup to lap nectar (Harris & Baker, 1958). The flowers open at night and emit an unpleasant smell which presumably attracts the bats. It should be pointed out here that visitation is not confined to bats only. Hawk moths have been observed to be frequent visitors. Furthermore, the pollination of the Sausage Tree has been recorded in several areas where bats are not found. The flowers are constructed in such a way that the male (four stamens) and female (stigma) organs are somewhat confined to the basal part of the tubular flower. The pollinators become effective only when they reach the inner portion of the flower in search of nectar.

The Silk-Cotton Tree or the Kapok Tree (*Ceiba pentandra*) is one of the most interesting members of the Bombacaceae in West Africa. In their studies of bat pollination, Baker and Harris (1959) note that when the flowers of *Ceiba pentandra* open, visits to them are made by *Epomophorus gambianus* (Fig. 8a), *Nanonycteris veldkampi* (Fig. 8c), and *Eidolon helvum*. They observe, however, that of these three bat species, *Nanonycteris veldkampi* is somewhat the most important visitor, since these bats stay on the trees much longer in search of nectar.

Another bombacaceous species that was studied by Harris and Baker (1959) is *Adansonia digitata* (Baobab Tree). A plant indigenous to the savannahs of West Africa, the Baobab occurs in large numbers in the Shai Hills area of the Accra Plains (Fig. 5b). The trees are in bloom during March to May, and at night some fruit bats such as *Eidolon helvum* visit the trees for the soft floral parts and presumably feed on the stamens and nectar as well.

The observation of bat activities on the above plants by Baker and Harris using still cameras, synchronized to electronic flashguns, in the 1950's exerted a profound influence on the students and faculty of the Department of Botany, University of Ghana, in pollination studies. However, with the departure of these plant biologists, pollination observations declined, although on occasions there were bursts of intensive studies by other faculty members.

PERSONAL OBSERVATIONS

My initial observations of plant and bat interactions were confined to the same trees and localities where Baker and Harris conducted their research, using more or less similar photographic techniques.

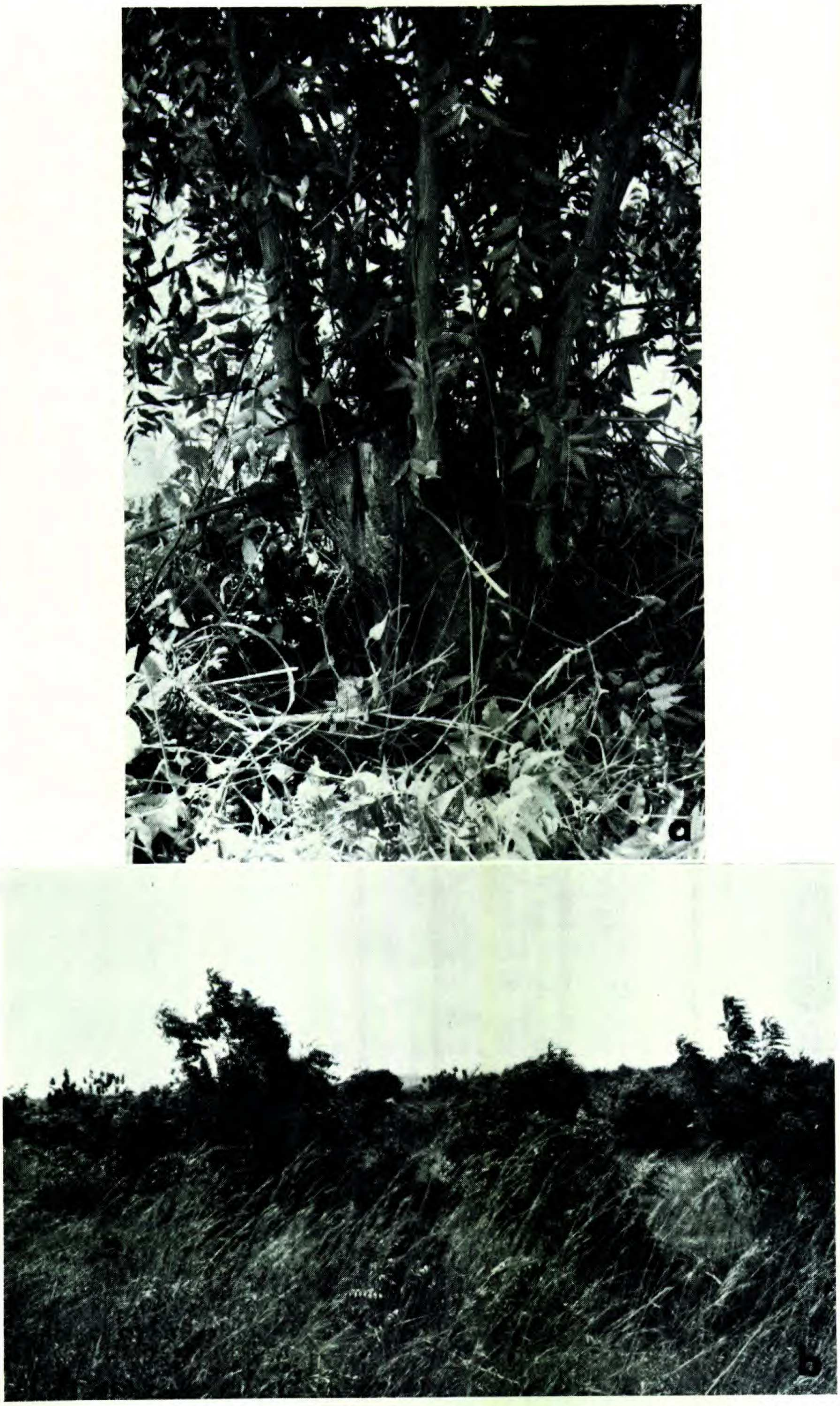


FIGURE 4.—a. The development of coppice after heavy pruning of *Azadirachta indica*.—b. Many young plants of *Azadirachta indica* growing in the Accra Plains.

With the advent of night vision equipment, modified for extended viewing of bat activities on plants, I began, on a daily basis, an intensive study of several plants that are visited by the fruit bats. The first night vision equipment I used was the Starlight Scope (the snooper scope), originally designed for modern night warfare. I had the good fortune of learning the potentialities and limitations of this instrument at the U.S. Army Electronics Command, Night Vision Laboratory at Fort Belvoir, Virginia. This instrument operates on the principle of magnifying available low level ambient light by 8,000 times without the aid of any artificial light source. While this instrument provided a marked improvement over the still camera documentation of bat activities, its limitations became obvious when I made attempts to use it in dense forested areas where even star light or moon light was in short supply.

More recently the Astrophysics Research Corporation of California developed new night vision equipment known as "The Owl Eye." This instrument permits the investigator to obtain high resolution photography (still and movie as well as video tape recordings) at ambient light sources of less than one or two candle power. This portable instrument (about 12 lbs.) has the capability of amplifying available light at an average of 20,000 times. Furthermore, it provided four times the detail obtained from regular television screens. These new instruments have greatly aided our observation of plant and bat interactions without interrupting the natural behavior of bats during their nocturnal activities.

Mangifera indica (Mango Tree).—This species probably originated in the Indo-Burma region, and its wild members occur in the northeast hilly forests of India (Purseglove, 1968). Until the beginning of the 18th Century mangoes were unknown in West Africa. They were introduced to this region by the Portuguese and are now common throughout West Africa. The fruits are exceptionally popular not only in India but in every country where the trees have become naturalized. The mango trees have widely branched terminal panicles that are 10–60 cm long with 1,000–6,000 flowers borne on new growth. Quite often both male and hermaphrodite flowers occur in the same inflorescence. The sweet-scented flowers are in cymes, 5–8 cm in diameter. The sepals are usually five, free, and yellowish-green in color. The petals are also five, but they are twice as long as the calyx. The petals are generally creamy in color with 3–5 dark yellow ridges on the inner surface. The stamens are usually five, inserted on the outer margin of a five-lobed disc, and only one or sometimes two are fertile. The anthers turn from pink to purple at anthesis. The pistil is abortive in male flowers, but in the hermaphrodite flowers both stamens and pistils are fertile. The fruits are in fleshy cups, variable in size (2.5 cm long) and come in a variety of shapes. Some are rounded, ovoid-oblong, or laterally compressed. The color is variable, and includes mixtures of green, yellow, and red.

The flowers of mangoes usually begin to open during the early hours of the morning and continue to open throughout the morning, reaching a maximum around noon. The anthers begin to dehisce either during or shortly after flower opening (Makherje, 1953; Mallik, 1957). The stigmas are reported to be receptive from just before the bud opens until 72 hours after the flower has opened completely. During the day the principal visitors to mango inflorescences are insects that feed on the nectar secreted into the disc situated between the corolla and the androecium. Pollination of the flowers is effected by the insects during feeding. The interaction of mangoes and bats observed in West Africa occurs when the fruits begin to ripen. Bats seldom visit mango trees when the fruits are unripe. I do not know if the ripe fruits emit some compounds that serve as attractants (odors) to the bats, but I am inclined to think that at dusk the visual appearance of the fruits has little influence in attracting the bats from a distance until they are fairly close to the mango trees.

On several occasions during the fruiting seasons (October to November) I observed large numbers of *Epomophorus gambianus* (Fig. 8a) in the Botanic Garden of the University of Ghana, virtually covering every available space on the large mango trees planted on either side of one of the main walks. These bats are fairly large, about 15 cm long with a wing span of about 60 cm. As the bat approaches the fruit, its wings' flapping action is considerably reduced. When it lands on the branch holding the fruit, the bat immediately attacks the hanging fruit. The skin of the ripe mango is first torn off, and the bat begins to feed on the juicy pulp. The bat generally feeds on the mango until the free flow of the pulpy juices is reduced, whereupon it moves on to another ripe mango to continue feeding. Throughout my studies I did not observe a bat carrying a mango from the tree. However, the enthusiasm with which the bat attacks the fruits causes considerable damage to the mango tree. It is not uncommon to find that after a mango tree has been visited by a huge flock of bats, over one-third of all the fruits on the tree will find their way to the ground, mostly destroyed.

The interaction between bats and mango trees, in which the plant offers food to the bat and gets nothing but destruction in return, can hardly be described as a mutualistic interaction. Generally when a mango tree is in fruit, there are panicles of flowers on the same tree. It may seem reasonable to assume that during feeding the bats may inadvertantly pollinate some of the flowers. I think, however, the chances for effective pollination are greatly reducd. Firstly, since most of the panicles contain both male and hermaphrodite flowers, the chances are that the flowers left on the mango tree during the height of fruiting may be the male flowers. Secondly, under normal circumstances it is known that 65–85 per cent of the hermaphrodite flowers remain unpollinated during the day (8:00 a.m. to 12:00 noon), when the stigma is most receptive to pollen. By nightfall, when the bats are active, I would imagine that the receptivity of the stigma could be sharply reduced (*cf.* Mallik, 1957; Singh, 1962; and Free, 1970). The only interaction that can be described as mutually beneficial in this case is the pollination of the mango flowers by the insects during the daytime and the food they obtain in the form of secreted nectar.

The relationship between bats and mangoes as I observed them in West Africa can therefore be described as a one-sided interaction. A cooperative interaction could have been the case, if there were some evidence that the bats either effected pollination during their visitation to the mango trees or were able to carry the heavy fruits and seeds off to other areas to ensure propagation. It is very possible that some of the fruits that fall to the ground are carried away by rodents and larger mammals. So long as the bats do not destroy the seeds,

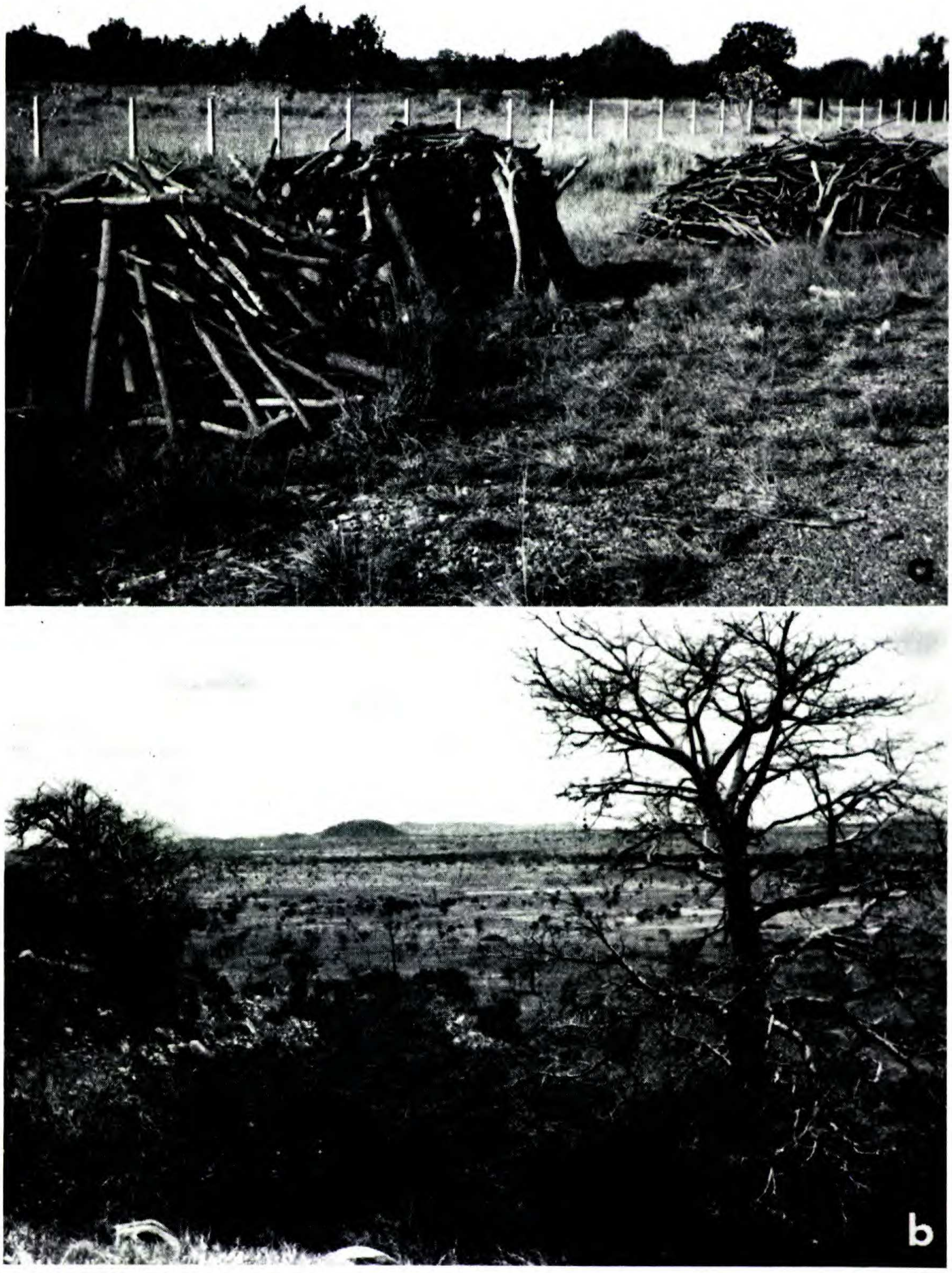


Figure 5.—a. A large supply of firewood obtained from the Neem Trees cleared in the Accra Plains.—b. *Adansonia digitata* growing on the Shai Hills overlooking a portion of the Accra Plains.

they may actually aid the dispersal by opening the outer covering and thus allowing the fleshy material to become more odoriferous and attractive to terrestrial dispersers.

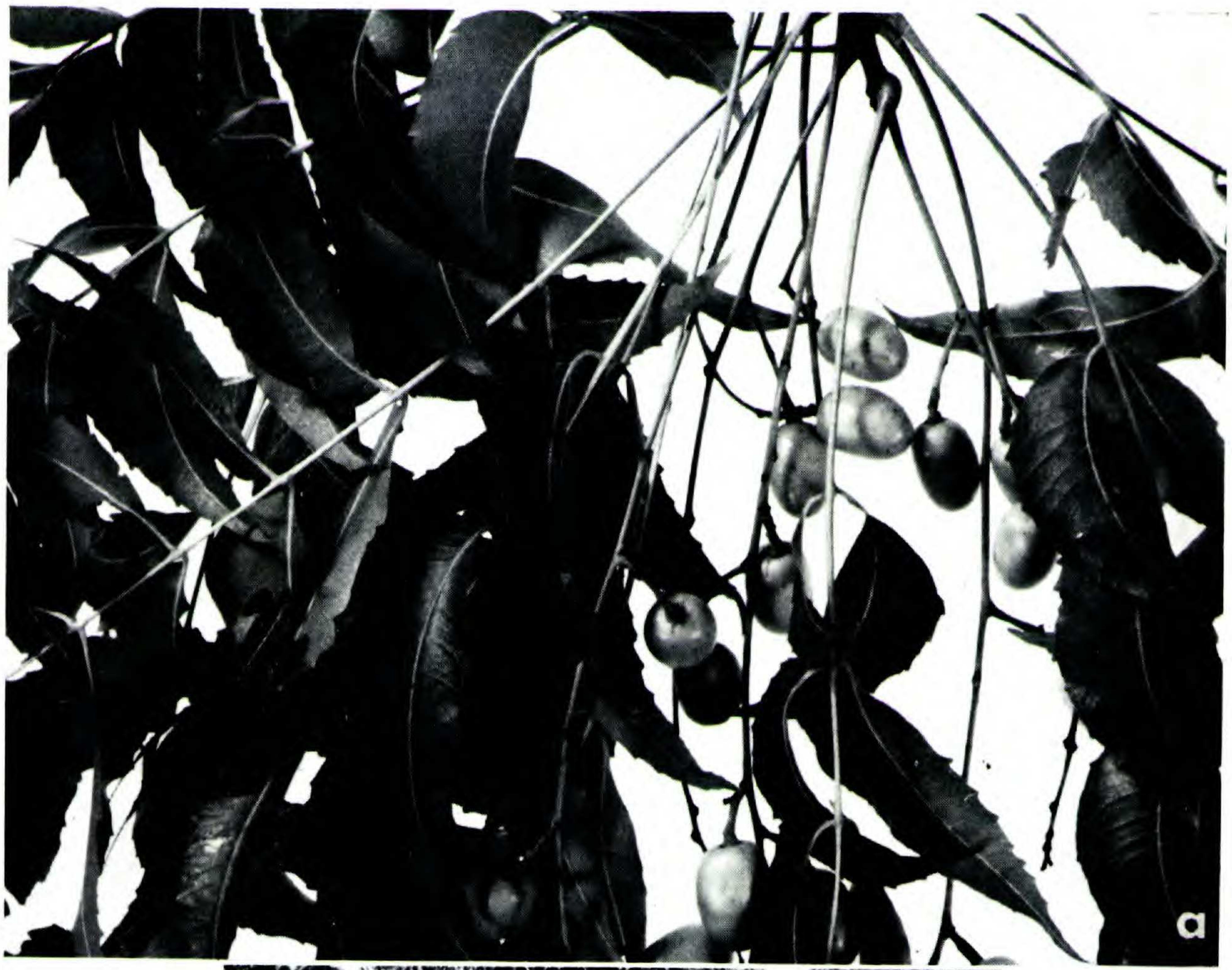
Anacardium occidentale (Cashew Tree).—In the back yards of homes where the cashew nut trees grow I have observed, on occasions, the visitation of these trees by bats such as *Eidolon helvum*, *Epomophorus gambianus*, and *Micropteropus pusillus*. The Cashew plant is an evergreen tree of tropical American origin. It grows to the height of about 12 meters. The bats visit this plant when the fleshy, swollen, edible pedicel, known as the cashew apple, is ripe and juicy. The bats feed on the cashew apple in the same manner as they do on the mango fruits. The cashew fruit, which is attached to the apple, is often left in place and not eaten by the bats. Several fruits and "apples" are destroyed during feeding. In the New World, bats are probably the primary dispersal agent for cashews. They carry off part of the pedicel and drop the hard nut when they are eating on the fleshy part (Wilson, 1971).

Ficus umbellata (Fig Tree).—At the botanical garden of the University of Ghana stand two large fig trees that are regularly visited by *Eidolon helvum* when the plant is in fruit (Fig. 7a). The trees are about 40 feet in height and provide abundant shade. The fruits are about one inch in diameter, borne in clusters on the branches of the tree away from the leaves. The fruits are green with pale spots on them. *Eidolon helvum* feeds on the ripe fruits night after night until fruiting is completed. The fruits are often carried in the bats' mouths to other roosting sites. They also spit out the seeds in flight or swallow them only to be excreted later. The trees also serve as a suitable meeting place for both sexes, where mating takes place quite frequently. I observed feeding and mating on the same tree on five consecutive nights in November 1972.

Psidium guajava (Guava Tree).—This plant is a native of tropical America, where it occurs wild and is also cultivated. The date of its introduction to West Africa is uncertain, however, fruit bats have found the fruits to be an important food source. The fruit is a berry, often with persistant calyx lobes. The fruit comes in a variety of sizes, some are globose, ovoid, or pyriform. They are from 4 to 12 cm long. The exocarp is light green to bright yellow. When ripe, the mesocarp is fleshy and juicy, ranging from sweet to tart with a distinct musky flavor.

Apart from large plantations, guavas are found in the back yards of houses in towns and villages in West Africa. When the fruits are ripe, fruit bats such as *Eidolon helvum*, *Micropteropus pusillus*, *Nanonycteris veldkampi* (Fig. 8c), and *Epomophorus gambianus* (Fig. 8a), feed on them. When a guava tree is near the roof of a house that is covered with corrugated iron sheets, the bats create continuous commotion by plucking the guavas with their mouths and dropping them on the roof while feeding. Some of the bats, such as *Eidolon* and *Epomophorus*, are capable of carrying whole fruits when flying and are thus able to distribute the seeds in nearby areas.

Carica papaya (Papaya or pawpaw).—The country of origin of this plant is not known, since it has never been seen wild. However, some botanists think that it must have originated in an area from southern Mexico to Costa Rica. Today the papaya is found throughout the tropical and subtropical regions of the world. The fleshy ripe fruits are eaten by man, birds, and bats. The fruit is a berry which is from 10–30 cm long, sometimes even longer. On the average a fruit may weigh about one kilogram. Fruit bats such as *Eidolon helvum*, *Epo-*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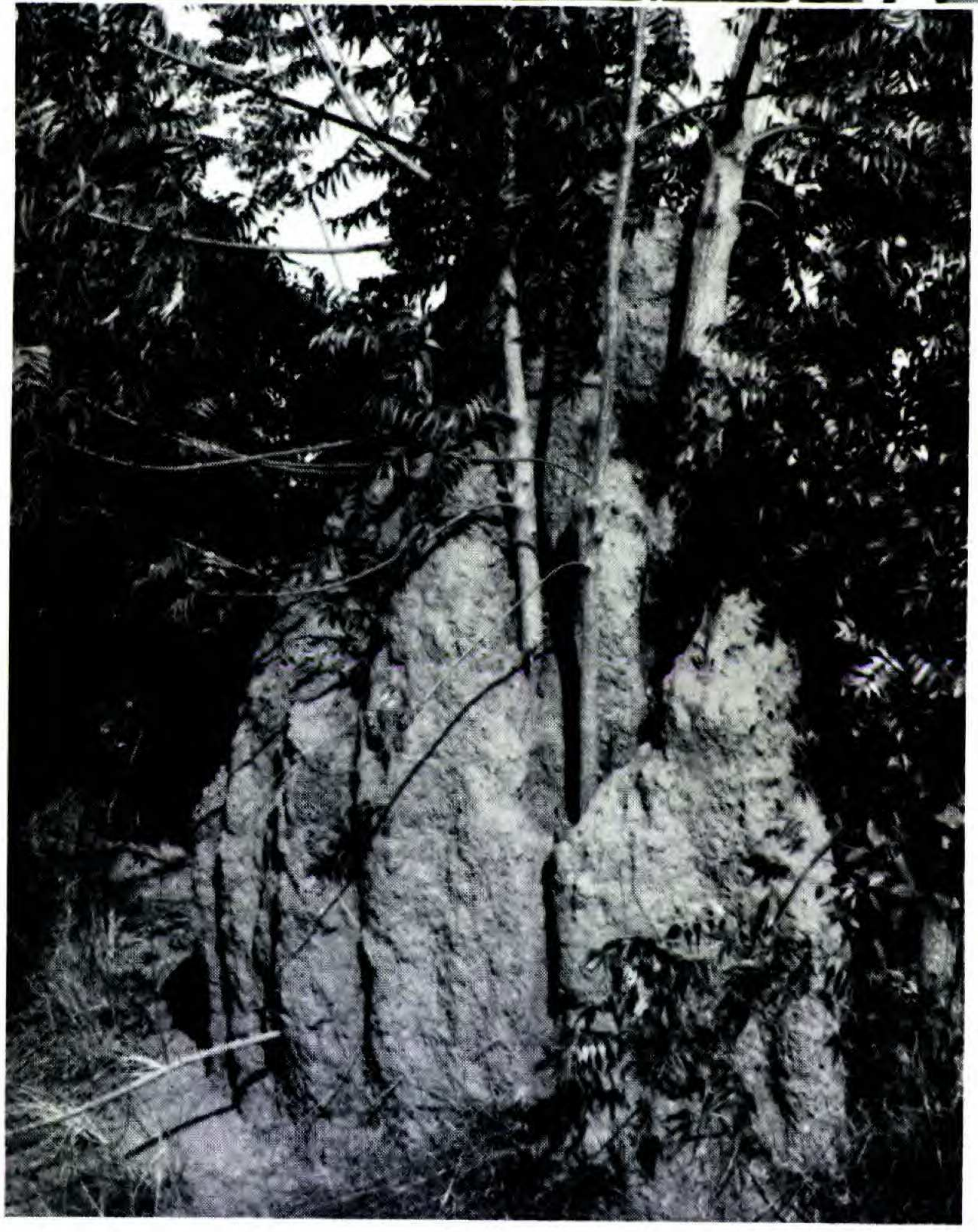

mophorus gambianus, and *Nanonycteris veldkampi* first bite the exocarp off and then feed on the inner fleshy part of the fruit. If the bat eats deeply into the fruit, it is likely to come in touch with the many black or greyish seeds which are attached to the inner wall of ovary. Seeds of *Carica papaya* germinate quite easily in 2 to 3 weeks. The viability of the seeds is long, some lasting for 2 to 3 years.

Kigelia africana (Sausage Tree).—One of the well known trees of the savannah woodlands of West Africa, this tree grows as high as 50 feet and is easily recognized by the hanging racemes of large, dark red or purple flowers. Harris and Baker's (1959) observations of the visitation of the long faced fruit bat (*Micropteropus pusillus*) as it lands on the lower tip of the flower and thrusts its head inside the flower to lap nectar is confirmed. On leaving the flower the bat is dusted with pollen which could easily be deposited on the stigma of the same or the next flower and thus effect pollination.

Spathodea campanulata (African Tulip Tree).—This is a spectacular tree which has large bright-red flowers with the edges of the corrolla lobes colored yellow. The flowering heads appear in circular masses with packed buds. The buds on the outer portion of the head open together, surrounding the inner buds. For several years I have observed in the University of Ghana Botanic Garden several bat visits to the avenue of *Spathodea campanulata* in the same vicinity as *Mangifera indica*. At dusk, *Micropteropus pusillus* insert their heads in the cup-like flowers to lap large quantities of rather dilute nectar. On several occasions I observed that instead of the bats entering the corolla tube, they conveniently tear the basal part of the flower cup and thus obtain an easy flow of nectar which they lap rapidly.

Azadirachta indica (Neem Tree).—Without a doubt the most interesting interaction between plants and bats in West Africa is demonstrated by this plant, commonly known as the Neem or Margosa Tree, and the Epaulet bat, *Epomophorus gambianus* (Fig. 3a). The Neem was introduced to West Africa from India during the British colonial days some sixty years ago as an exotic forest tree, together with other plants such as *Cassia siamea*, *Cedrela mexicana*, *Gmelina arborea*, and *Tectona grandis* (Lane, 1958). The idea behind the introduction was to supplement the indigenous species with exotic species that might be useful in the economic activities of the West African countries. The British silviculturists carefully worked out various techniques for the establishment of the introduced species. These were based on the climatic conditions of the regions, soil types, and the conditions of the vegetation zones. Nurseries were established to raise the plants for transplanting. Generally after 9–12 months, the young plants were transplanted to selected areas within the countries. In Ghana, for example, the young trees were planted in both the high forest and the woodland-savannah zones. In the Accra-Achimota area a large acreage of Neem Trees

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FIGURE 6.—a. Leaves and fruits of *Azadirachta indica*.—b. Termite mound surrounding a Neem Tree in the Accra Plains.

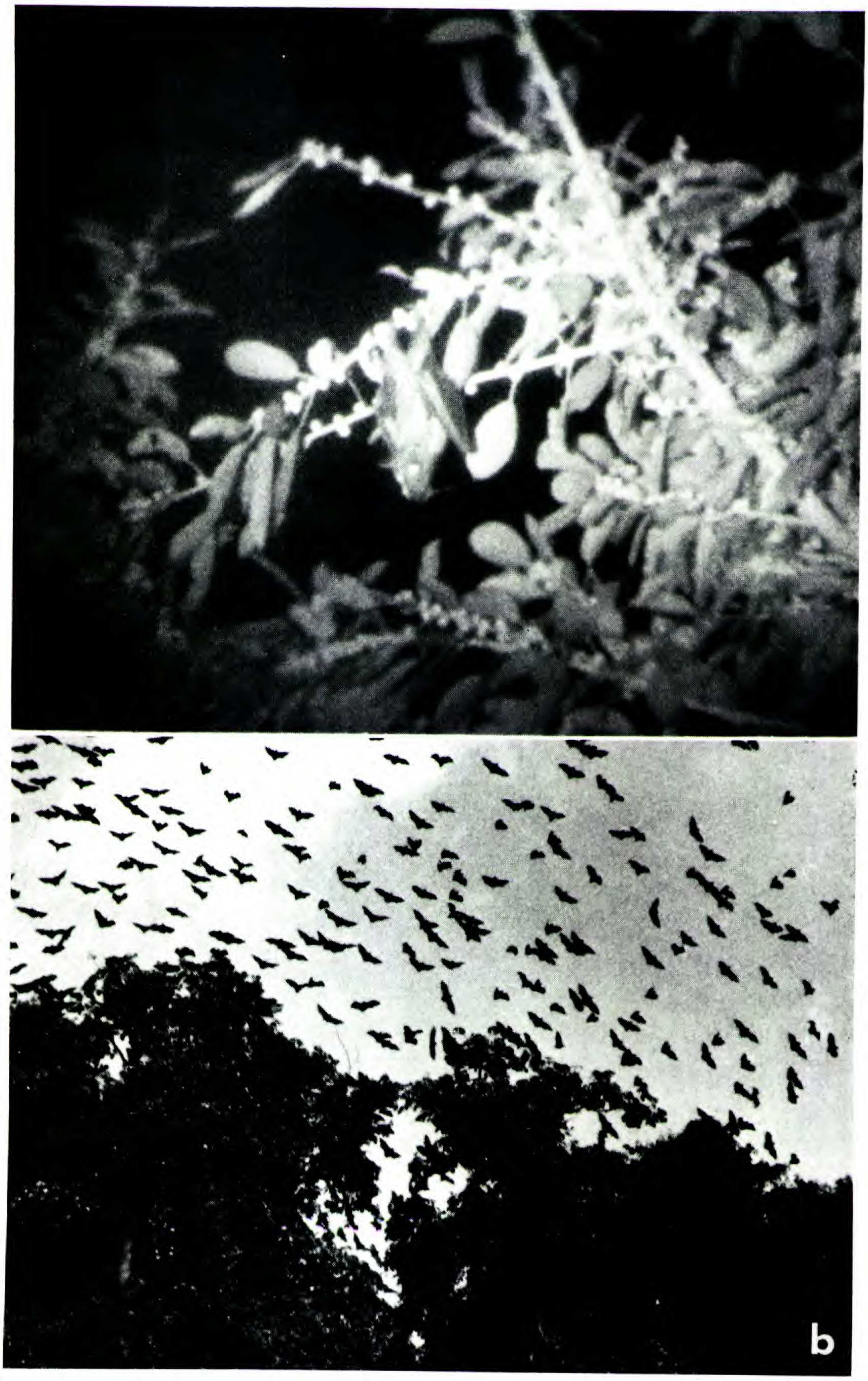

Figure 7.—a. *Eidolon helvum* feeding on fruits of *Ficus umbellata*. Photograph taken through "The Owl Eye" night vision equipment.—b. A large flock of *Epomops franqueti* leaving their roost at dusk to feed.

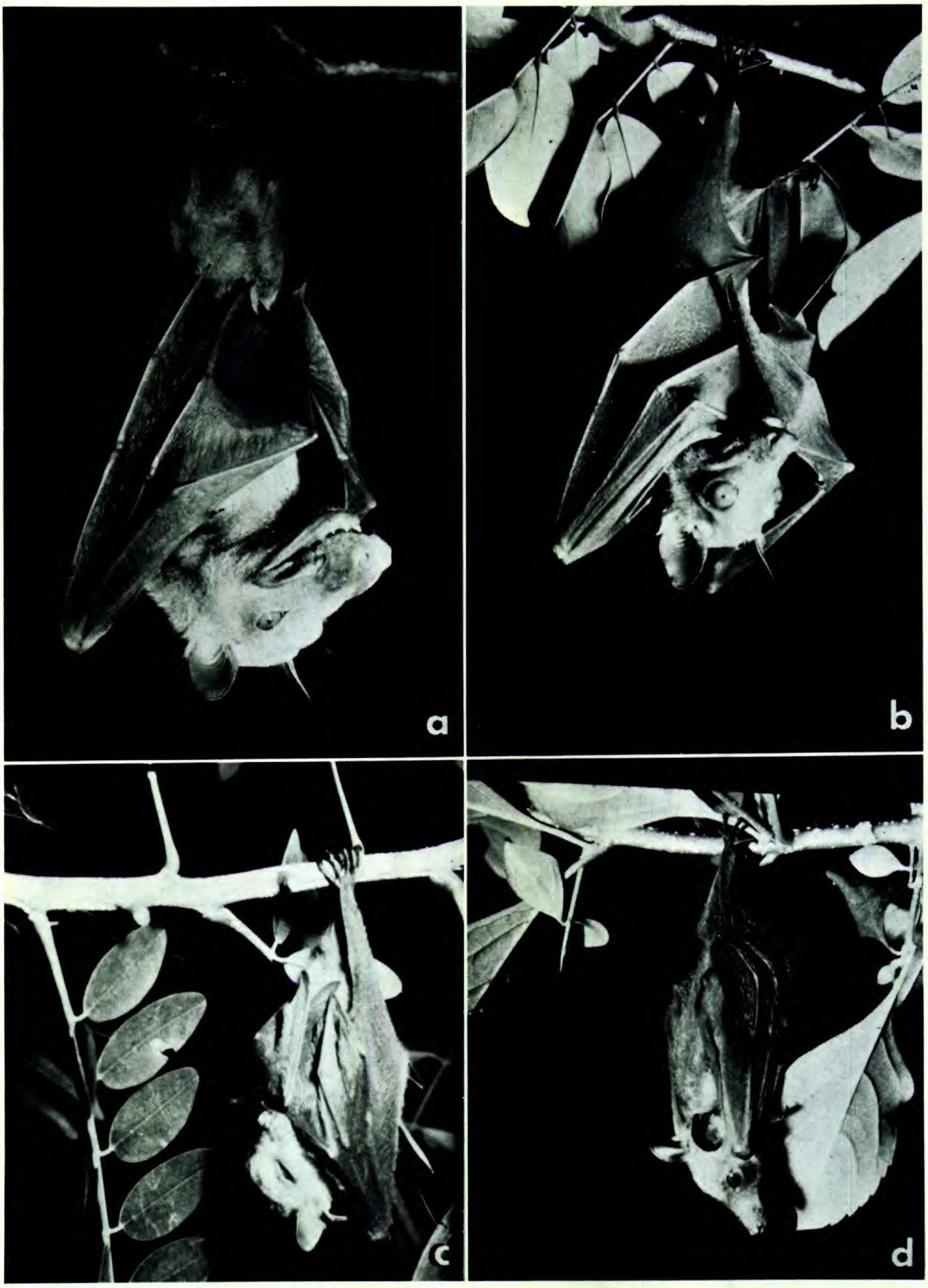

FIGURE 8. General morphology of West African bats.—a. *Epomophorus gambianus.*—b. *Epomops franqueti.*—c. *Nanonycteris torquata.*—d. *Megaloglossus woermanni.*

was planted. This plantation became a forest reserve after a number of years. The trees grow to 80 feet high and have a dense crown. The leaves are pinnate, glossy, and with slightly toothed margins (Fig. 6a). The flowers are white, small, and scented. After five years the plants begin to flower and fruit profusely. The majority of the seeds are viable and need no pregermination treatment. The ellipsoid fruits (Fig. 6a) are about 1.2 cm long with a fleshy outer coat and sweet juicy pulp.

Epomophorus gambianus are perhaps attracted to the Neem Tree more than any other West African fruit bat. *Eidolon helvum* also visit the Neem to feed on nectar and fruits. At dusk these bats leave their roosting places and converge in the forest reserve as well as the several acres of Neem Trees planted as "amenity" trees in towns and villages throughout the country. The bats feed for long periods; sometimes a flock will stay on a tree for at least one hour before flying away. During their departure, however, many of them carry neem fruits in their mouths and drop the seeds during flight before or after they have completed feeding on the fruit.

ROOSTING CHARACTERISTICS OF *EPOMOPHORUS*

It is generally observed that bats in West Africa have the tendency to roost on trees near villages and towns as well as the outskirts of these areas. One of the introduced tropical trees that has become a favorite roosting haven for the bats is the Neem. It seems that the bats use the Neem Tree for two separate functions: (a) during the day to roost in them and (b) at night to feed on the fruits. One interesting phenomenon is that although neem fruits are available on the tree on which the bats roost, they are not eaten. As soon as it is dusk the bats begin to fidget, especially when there are signs of encroachment of one's territory by another bat. The bats begin to hover around the tree for about 2 or 3 minutes, and then take off en masse to their selected feeding area. Intensification of the fidgeting behavior, which comes at sunset, provides the signal to which the bats respond in preparation for their flight to the feeding area. Similarly, the *Eidolon helvum* that roost in the palms in Ghana do not feed on the fruits of the same palm tree, but fly to another palm to feed. "This seems to be a general phenomenon. We noticed that the bats in Ghana did not roost in trees of *Ceiba* or *Parkia* that they pollinated or *Ficus umbellata* that they visited for fruit. But it is *most* interesting that they do not even eat neem fruit when this is available at their roost" (Dr. Herbart Baker, personal communication). A possible explanation of this peculiar behavior is that when the bats return to roost from feeding, they are most likely well fed, and therefore they need no more food during the roosting period. By dusk, however, the bats respond to their daily (circadian) biological clocks that "instruct" them to fly to their feeding grounds. This normal and natural behavior precludes the bats from remaining on the same tree to feed.

EFFECT OF FEEDING ON DISPERSAL OF SEEDS ON THE ACCRA PLAINS

In the mid-1950's the silviculturists in Ghana (then the Gold Coast) discussed the potentialities of planting *Azadirachta indica* on the Accra Plains to produce some form of an irrigated plantation. The Accra Plains forms a major part of the Ghana coastal savannah-grassland area which covers a sizable portion of the southeastern part of the country (Fig. 2). The northwestern part of the Plains is limited by the Akwapim escarpment to the northwestern side by the Volta River. The southern part of the Plains is bordered by the Atlantic Ocean, but more specifically the Gulf of Guinea. The rainfall is comparatively low, averaging 25–30 inches annually. Ecologically, the Accra Plains is most interesting in that it is quite different from the Guinea savannah or any other vegetation types of the coastal woodland-savannah composition, such as the Cape Coast-Winneba Plains. The Accra Plains is generally undulating for the most part, but on the northeasternmost part of the coastal section stand the prominent Shai Hills with a sizable population of *Adansonia digitata* (Baobab Trees). The vegetation of the rest of the Accra Plains is composed of grasses such as *Andropogon gayanus*, *Panicum maximum*, *Ctenium newtonii*, *Enteropogon macrostachyus*, *Microchloa kunthii*, *Setaria sphacelata*, and trees and shrubs such as *Sida cordifolia*, *Mimosa pigra*, *Waltheria indica*, *Elaeophorbia drupifera*, *Dichrostachys glomerata*, *Griffonia simplicifolia*, *Securinega virosa*, *Croton lobatus*, *Indigofera hirsuta*, and *Hoslundia oppositofolia*.

None of these trees, however, have become dominant on the Accra Plains. One of the spectacular features of the Plains is the many pronounced termite mounds (Fig. 6b), and these are usually colonized by shrubs and trees. With the introduction of *Azadirachta indica* planting near Achimota and the western edge of the Accra Plains, it was soon realized that the potential of this plant as plantation material was very high.

The original need for planting *Azadirachta* and *Cassia* was to have a wood supply available on a continuous basis (Fig. 5a). Firewood plantations were thus established on an eight-year-rotation system for *Azadirachta* and on a five-year-rotation system for *Cassia*. In the case of the Neem, the plots were arranged in such a way that when the first plantings were eight years old, the eighth-year plantings were one-year-old. At the end of the first eight years, the trees in plot one were cut almost to the ground, leaving about a foot of the tree stump on the ground. Since the Neem grows freely, such heavy pruning was considered necessary to reduce excessive coppice (Fig. 4a). After the initial plantings the project was not continued, but it soon became evident that sporadic seedlings of the Neem were appearing on the whole of the Accra Plains, with a high percentage of the seedlings appearing just outside the plantation and tapering towards the eastern part of the Plains up to the foot of the Shai Hills.

For several years I have wondered about the encroachment of Neem Trees on the Accra Plains. During my observations of the nocturnal flight patterns of bats from their roosts in and around the University of Ghana campus to the Achimota Forest Reserve (composed primarily of Neem Trees and Cassias) where they feed, it became obvious that from the forest reserve the bats flew across the Accra Plains and dropped neem seeds. It is now evident that substantial scattering of Neem Trees on the Accra Plains should be attributed to the dispersal of seeds by fruit bats. When the bats cross the Accra Plains, after

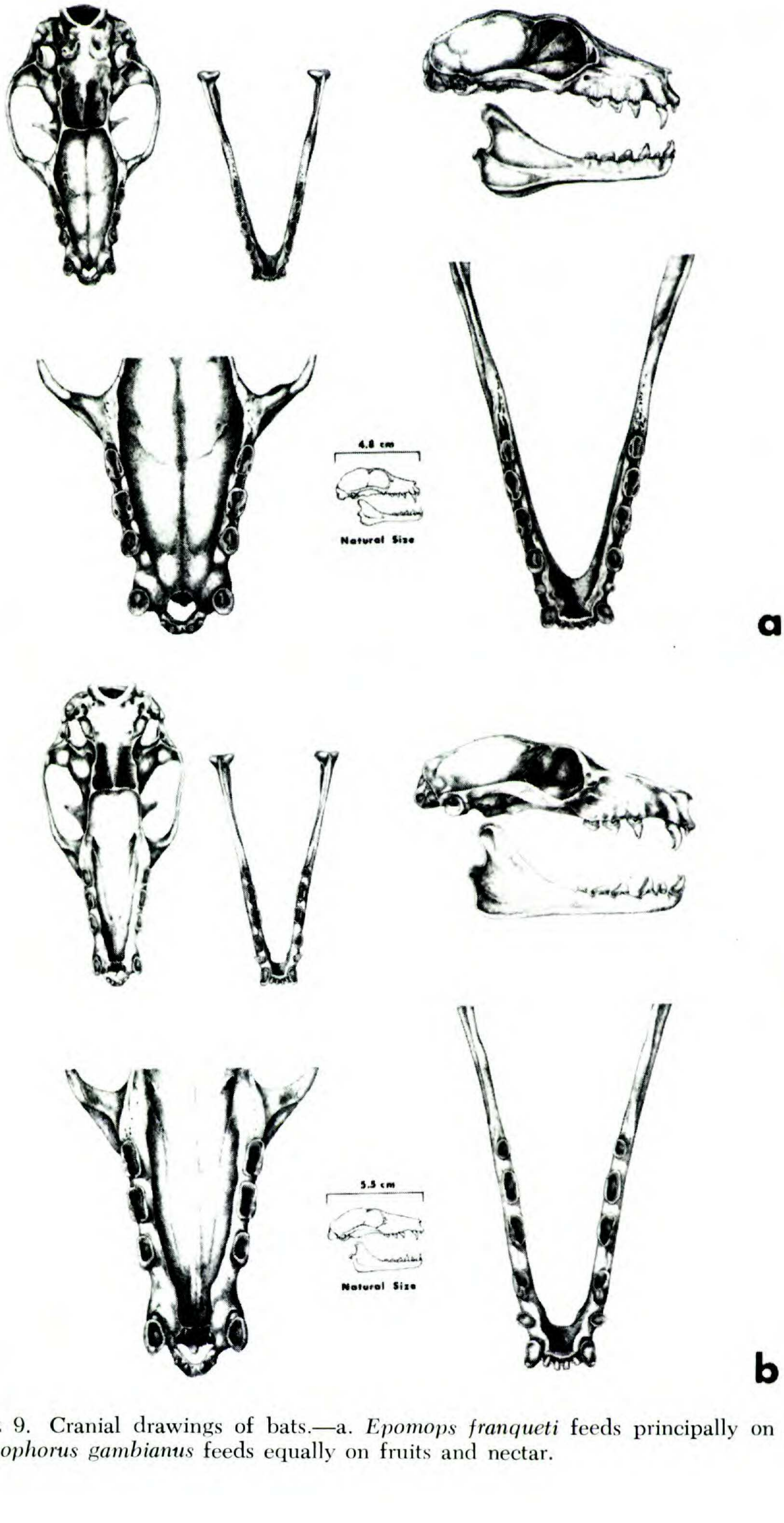

FIGURE 9. Cranial drawings of bats.—a. *Epomops franqueti* feeds principally on fruits. —b. *Epomophorus gambianus* feeds equally on fruits and nectar.

making several stops on the way, they reach the Shai Hills (Fig. 5b) and engage in another intensive feeding on the flowers of *Adansonia digitata* as well as on the fruits of *Azadirachta indica.* The bats return to their roosts in the early hours of the morning, quite often in small groups instead of the large flocks that leave the roost at dusk to feed.

EFFECT OF INTRODUCED PLANTS ON BATS

The question is often asked: On what kinds of food did the bats feed in West Africa before the introduction of exotic plants such as *Azadirachta indica, Mangifera indica, Carica papaya,* and *Psidium guajava*?

To answer this question meaningfully will require a brief review of the evolutionary trends in the feeding mechanisms of bats. In a recent paper Baker (1973: 147) pointed out that "the term 'co-evolution,' so freely used nowadays, may not be the most apt in describing the correlated development of flowering plants and flower-visiting animals over a period of time. The evolutionary pattern must be one of *demande et réponse* which, if prolonged, may produce a 'reciprocating' evolution, wherein changes in one kind of organism stimulate the selection of alterations in the morphology or behavior of another kind of organism, to be followed by a return influence in the first kind of organism. In such responsive or reciprocating evolution (at least insofar as it involves pollination relationships), it appears to be the animals that more often make the initial selective demands and the plants that show the most profound responses."

It is generally accepted that the earliest known bats (from middle Eocene to Oligocene) were insectivorous with dentitions similar to many recent members. The structural modifications of the teeth, the muzzle, and the tongue of fruit bats represent derived and specialized conditions. We can speculate that with the arrival of flowering plants, bats began to pursue insects that visited fruits and flowers. Consequently, some of the bats became interested in floral nectar and fruits, hence the process of structural modifications over an extended period of time. For further explanation see Baker (1973: 156).

In the absence of any definitive studies on this subject, we can only surmise that in West Africa, for example, bats were initially insectivorous (although this might have happened before the bats reached West Africa), but through time some became adapted to feeding on floral parts and nectar and some became totally frugivorous, thus feeding on fruits of all kinds. The dentition of West African fruit bats shows quite clearly that the sharp cusps of the molars have been suppressed and the crowns significantly broadened or in some cases clearly flattened. Such dental modifications are the result of constant crushing and mashing of fruits and nuts by bats to ensure smooth mastication of food. In a recent study Wilson (1973) presented a quantitative analysis of food preferences of several genera of bats. A comparison of skull shape and dentition on the one hand and the percentage of food preference on the other (Table 1) give some indication of correlation between muzzle morphology and feeding habit. Bats that feed principally on fruits, such as *Epomops franqueti* (Fig. 9a), *Eidolon helvum* (Fig. 10a), *Myonycteris torquata* (Fig. 11a), *Scotonycteris ophiodon,*

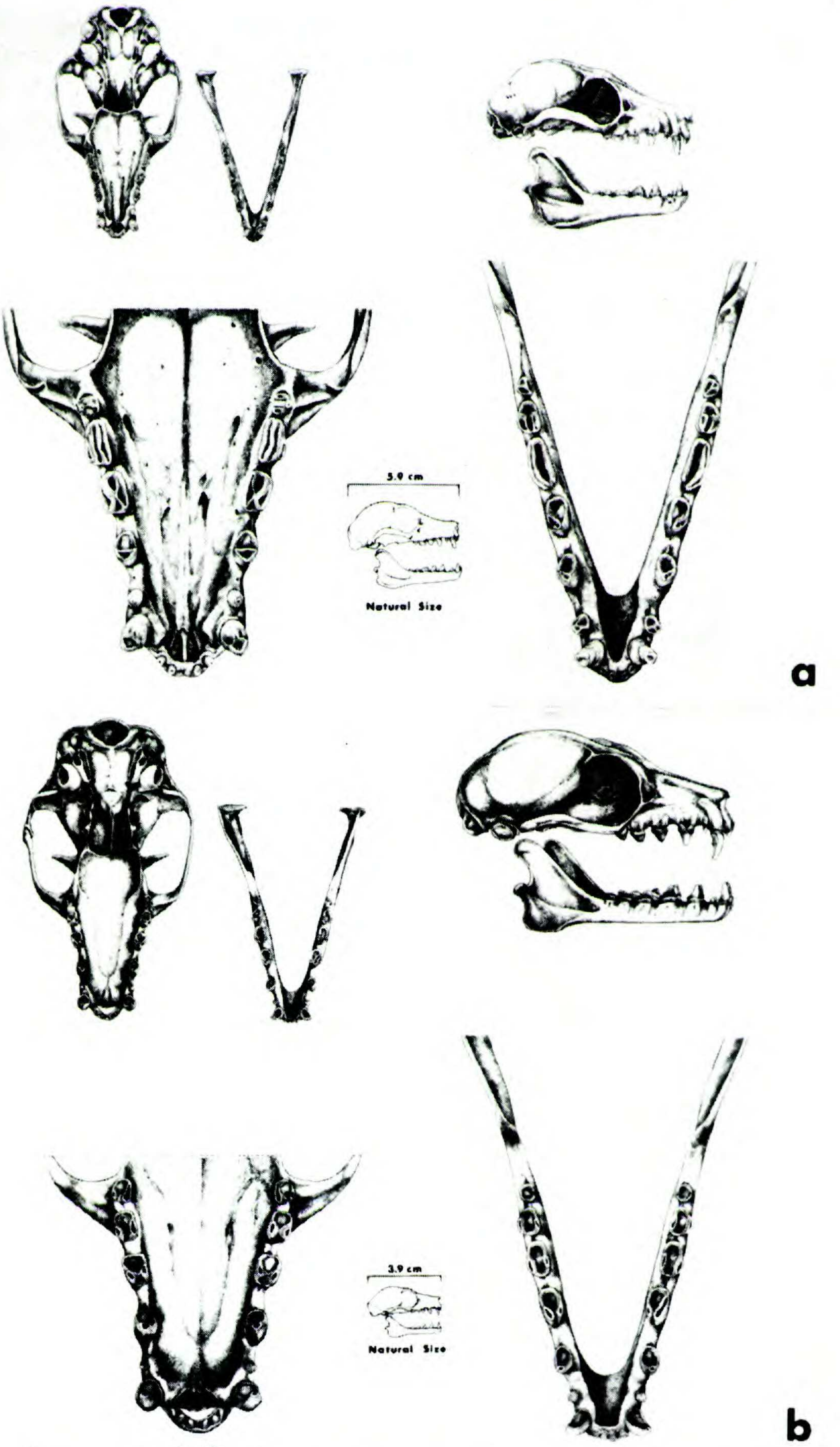

FIGURE 10. Cranial drawings of bats.—a. *Eidolon helvum* feeds principally on fruits.—b. *Rousettus aegyptiacus* feeds equally on fruits and nectar.

TABLE 1. Percentage food preference of West African fruit bat genera and New World *Desmodus*. Data from Wilson (1973: 16–18).

Genus	Fruit	Nectar	Foliage gleaning	Blood
Myonycteris	100	–	–	–
Eidolon	90	10	–	–
Epomops	90	10	–	–
Scotonycteris	90	10	–	–
Hypsignanthus	80	20	–	–
Micropteropus	80	20	–	–
Epomophorus	50	50	–	–
Rousettus	50	50	–	–
Megaloglossus	–	100	–	–
Nanonycteris	–	100	–	–
Desmodus	–	–	10	90

Hypsignanthus monstrosus (Fig. 11b), and *Micropteropus pusillus* (Fig. 12a), have short muzzles in comparison with predominantly nectar-feeders such as *Megaloglossus woermanni* (Figs. 8a, 13a). Bats that feed equally on fruits and nectar such as *Epomophorus gambianus* (Fig. 9b) and *Rousettus aegyptiacus* (Fig. 10b) have muzzle shapes that lie between the two extremes.

In contrast to the dentition of the frugivorous and nectarivorous bats is the highly modified dentition of the vampire bat (*Desmodus rotundus*) of the New World Tropics (Fig. 13b). The sharp but numerically reduced teeth are designed for slicing the surface of the skin to allow easy flow of blood which is its main diet.

It seems reasonable to assume that before the introduction of trees such as the neem, mango, cashew, papaya and guava, West African fruit bats lived on flowers and fruits native to this region, such as *Butyrospermum parkii* (Shea Butter Tree). This deciduous tree, which is common in the savannahs of West Africa, produces white flowers that are clustered at the ends of the shoots and one-seeded fruits about 4–5 cm long with fleshy pulp. The bats feed on this fleshy pulp, releasing the seeds that fall to the ground where, after the fleshy pulp decomposes, the seeds are gathered by man. After drying, the seeds are pressed locally for the fat (45–60 per cent) and protein (9 per cent). Most shea nuts are exported to a number of European countries where the extracted oil is used for production of soaps, candles, and cosmetics and as a constituent of chocolate fillings in creams (Purseglove, 1968).

We might assume that food was not so abundant as it is today and the population of fruit bats therefore not so dense as it is now. In the open skies of the Accra Plains it is not uncommon to observe large flocks of fruit bats covering a quarter of a square mile almost every evening. The availability of food in this savannah-woodland region has seemingly helped to increase the population of the fruit bats which in turn continues to ensure the progressive propagation of seeds such as those of the neem tree (Fig. 4b).

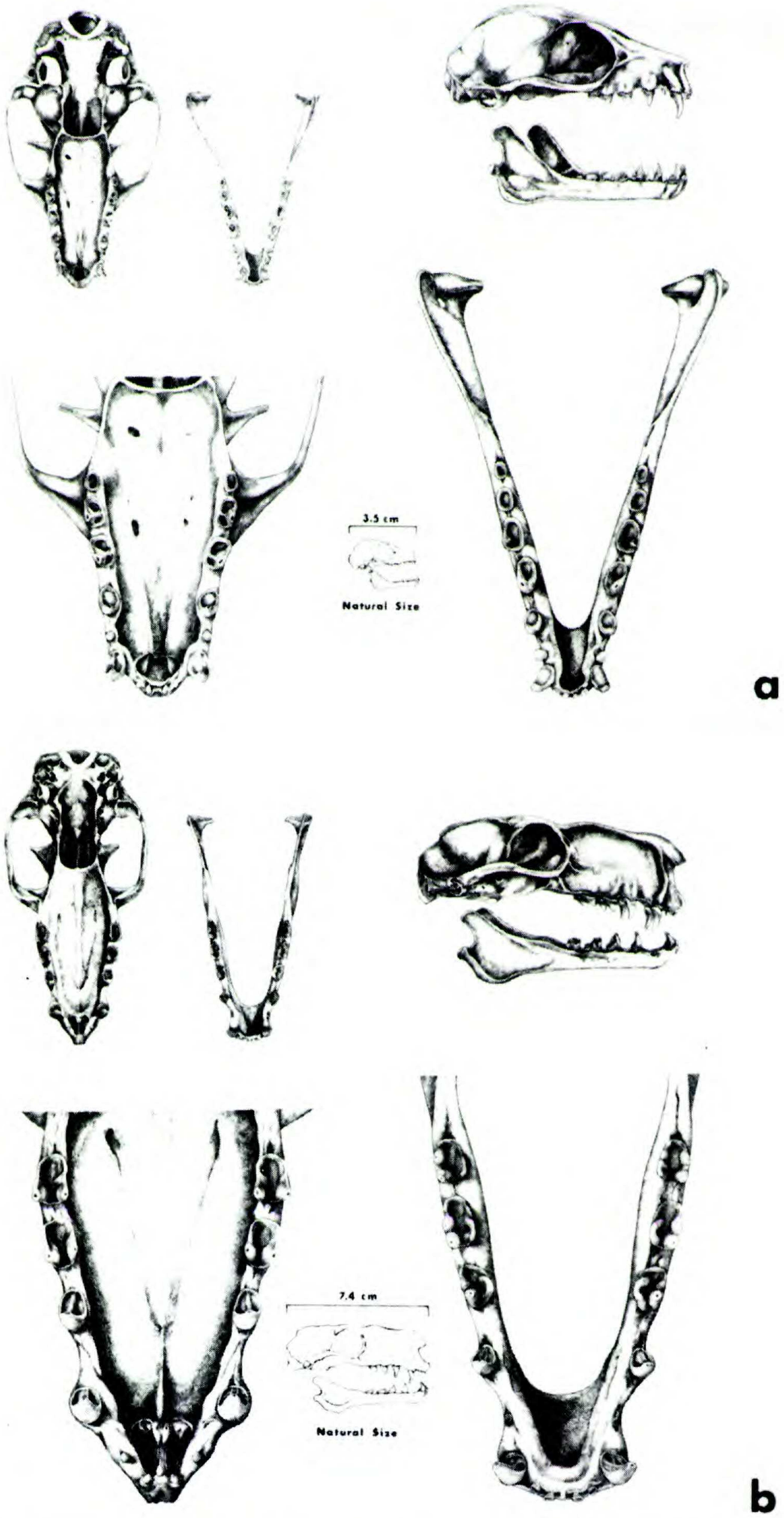

Figure 11. Cranial drawings of bats.—a. *Myonycteris torquata* feeds exclusively on fruits.—b. *Hypsignanthus monstrosus* feeds mostly on fruits.

Advantages and Disadvantages of Plant and Bat Relationships

Some of my observations which deal with the interrelationship between plants and bats have been alluded to above. I will now attempt to classify the various interactions in a way that will demonstrate the effect of plants on bats and vice versa from both the positive and negative viewpoints.

Effect of bats on plants—positive aspects: Fruit bats have been instrumental in effecting the pollination of some flowering plants whose flowers open with maximum anthesis at dusk and at night while the stigma is also receptive to pollen during this period. Although moths, bees, beetles, and butterflies participate in various pollination activities, these bats have been found to be very important during their nightly visits to plants such as *Parkia clappertoniana*. Similarly, the fruit bats visit *Ceiba pentandra* in search of nectar and floral parts. In the process the conspicuous pollen grains of the flowers are carried on their fur from one flower to another on the same tree, thus promoting autogamy and geitonogamy, or they may carry pollen from one plant to another and effect allogamous pollination. Furthermore, the ten or so hours of pollinating activity by bees during the morning are supplemented at dusk by bats, for the flowers of the kapok tree remain open for some 20 hours. The flowers of *Kigelia africana* also open at night, and among its visitors are hawk moths and bats, such as *Nanonycteris veldkampi* and *Micropteropus pusillus*. Some members of *Kigelia* occur, although not naturally, in regions that have no fruit bats, and their flowers are pollinated either by moths or artificially by man. In areas where the bats occur in addition to the moths, there is ample evidence that the bats play an effective role in the pollination of *Kigelia africana*.

Another positive relationship between bats and plants is seed dispersal that takes place during feeding by frugivorous bats. The dispersal of neem fruits and seeds of the Accra Plains by *Epomophorus gambianus* and *Eidolon helvum* is a classic case of *mutualistic* existence between two organisms—the bat obtaining its sustenance from the ripe neem fruits while ensuring the continuous propagation of this plant.

Negative aspects: Tremendous enthusiasm is generally engendered by bats when they leave their roosts to go feeding. This often results in a considerable amount of fruit and floral destruction of the roost tree.

As I have indicated earlier in this paper, it is not uncommon to find over one-third of the ripe fruits underneath a mango tree after it has been visited by bats. I always ponder over the thought of what the economic consequences on the West African cocoa producing countries would be if the frugivorous bats were feeding on cocoa fruits. However, I do not know of any accounts of bat destruction of cocoa pods, except for Hicks' (1967) report that bats and birds caused the loss of 8.7% of cocoa pods in a New Guinea orchard.

Bats frequently select certain trees in which they roost over a period of several months, and their continuous roosting often results in sustained damage to these trees. For example, several royal palms in which bats roost in Ghana have been killed because of continuous urination by bats in the crowns of these trees. Henshaw (1970: 226), in discussing special environmental parameters for bats,

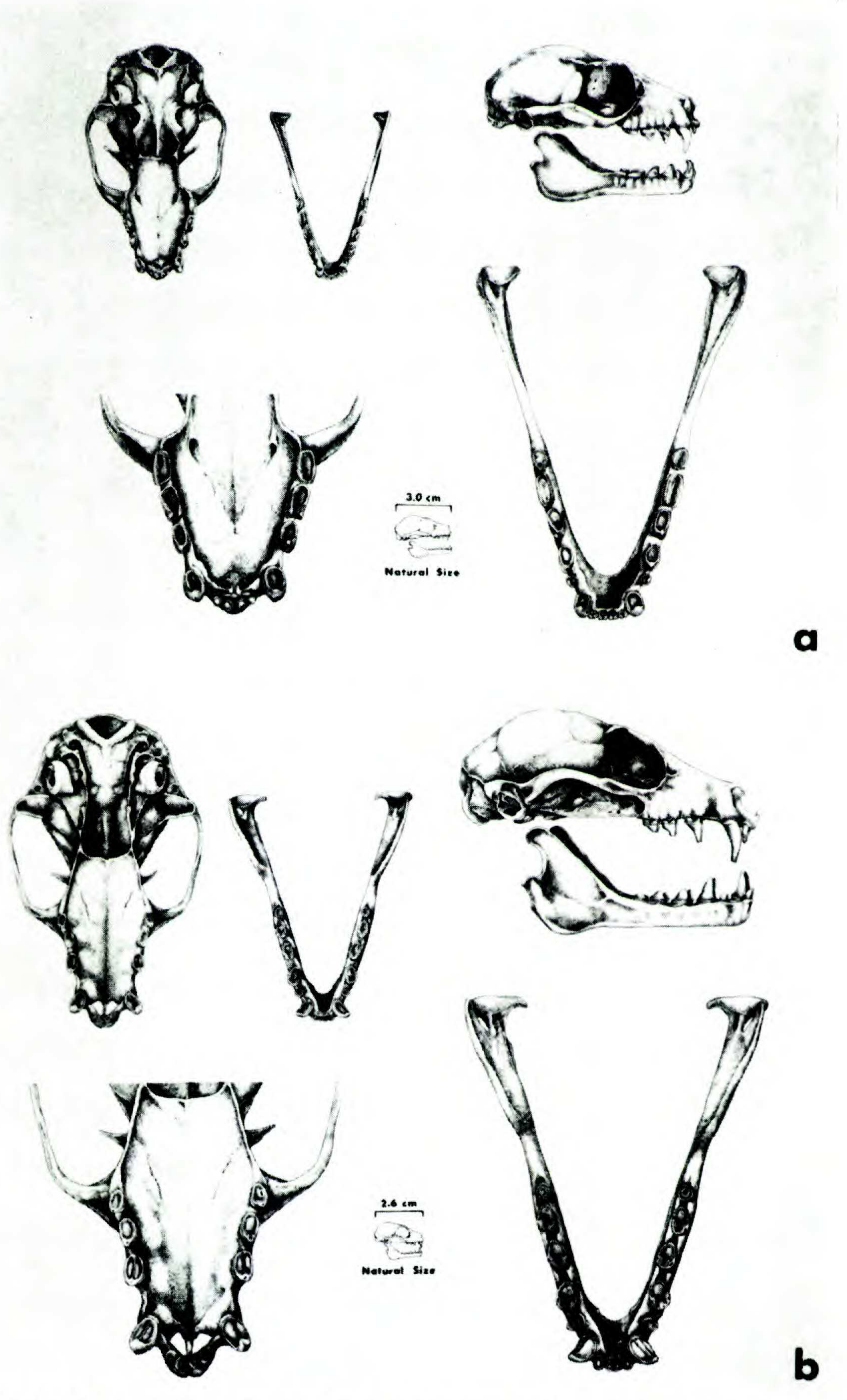

Figure 12. Cranial drawings of bats feeding principally on fruits.—a. *Scotonycteris ophiodon*—b. *Micropteropus pusillus*.

mentioned among other things that the microhabitats of some of the bats may provide "a number of potentially stressful environmental conditions for which animals may have produced physiological adaptations." He pointed out that the partial pressure of oxygen in caves which *Tadarida brasiliensis* inhabit may be lowered while the partial pressure of carbon dioxide may be raised, resulting in the concentration of ammonia. It seems reasonable to assume that the high concentration of ammonia, which results from bacterial decomposition of the urine in such an environment, frequently reaches toxic levels strong enough to kill the vegetation. I have also observed that the Neem Trees in which the bats roost often grow vegetatively for long priods when most other trees of the same species are flowering and fruiting. I presume that the high concentrations of toxic material may have some adverse effect on the flowering of the specific trees.

Effect of plants on bats—positive aspects: It is well known that the bats often live in dark caves and in crevices or roost on trees that have very dense foliage such as the neem and the palm trees. Even those bats that are tolerant of daylight tend to cluster in the darkest portion of a tree that has otherwise scanty foliage. The trees provide shelter for the bats most of the day as well as protection from their predators. By far the most important contribution of the plants to the existence of frugivorous bats is to provide them with food such as nectar, floral parts, fruits, and nuts. The availability of an abundant food supply will often improve the breeding conditions of the bats and thereby increase their numbers.

Adverse aspects: It is very possible that a continuous food supply may have an adverse effect in delineating the roosting areas of the bat population in some regions. For example, the trees in the area of the Lilidze Mountain Range (this mountain formation separates Ghana from Togo) on which some bats roost are so congested that large numbers of *Epomops* (Fig. 7b) have resorted to roosting on bare rock surfaces (Fig. 3b). These bats are therefore subjected to high solar radiation. However, they have devised a system of alternating roosting and flying throughout the day, while those bats roosting in trees at the same place continue to enjoy seemingly uninterrupted roosting during the same period. Notwithstanding, bats will often adapt to the optimum combination of food and roosting sites, no matter how adverse the roosting sites. If the rock roosts are sub-optimal, it will affect the reproductive effort of those bats using them, and natural selection will work to either better adapt them to the roosts, or lower their population size.

In evaluating the rapidly changing environment of the Accra Plains in response to the continuous dispersal of neem seeds by bats, I have considered the impact of *Azadirachta indica* on the native plant population and the rodent and other faunal organisms that inhabit this region. It seems clear to me that the progressive occupation of the Accra Plains by the Neem Trees—barring any major ecological catastrophe—may diminish or destroy the equilibrium between the native flora and fauna. Recent faunistic studies of parts of the eastern Accra Plains have shown that in areas where large populations of Neem Trees occur, native rodent populations have diminished considerably (Dr. Henry Setzer, per-

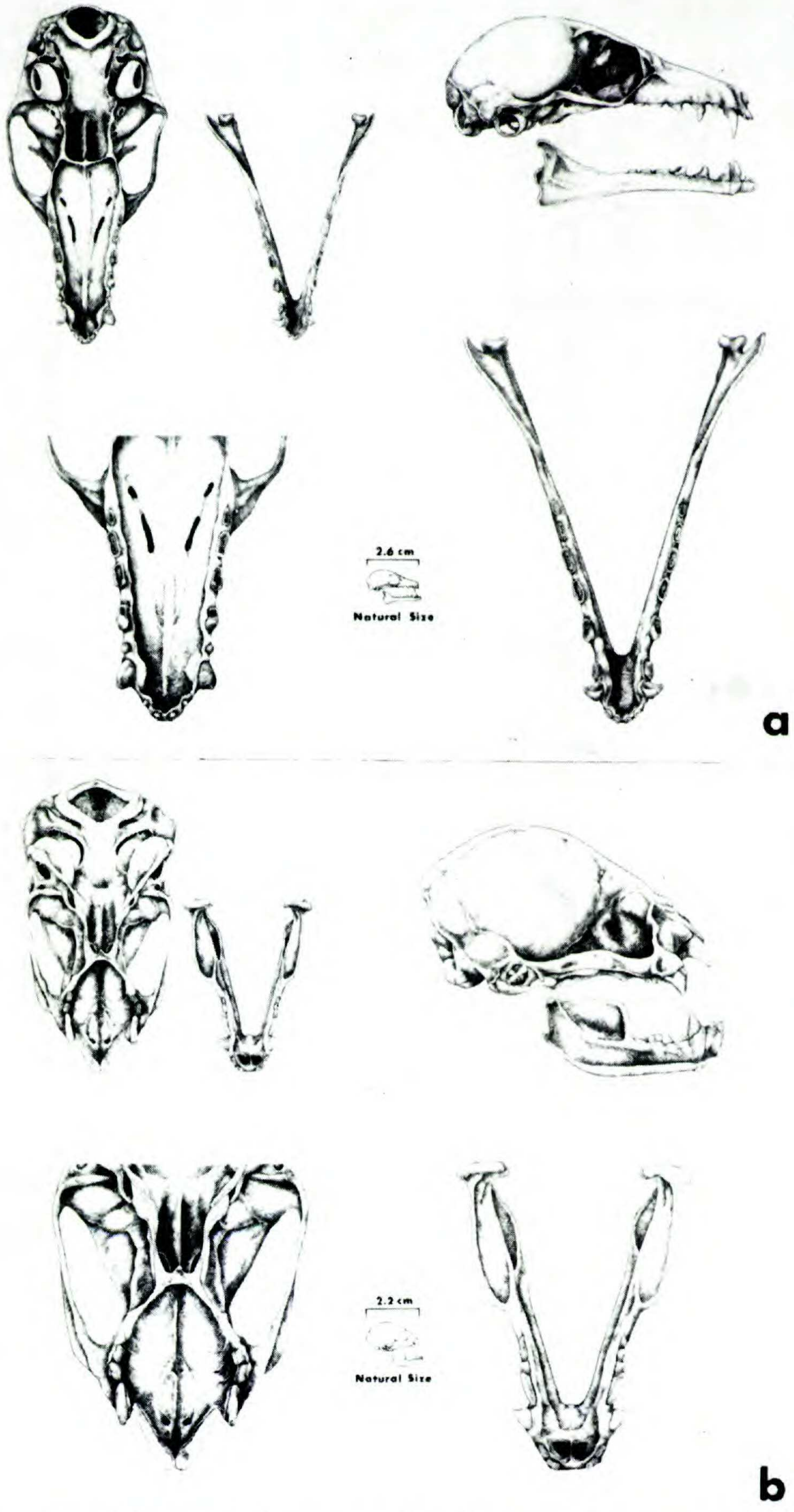

Figure 13. Cranial drawings of bats.—a. *Megaloglossus woermanni* feeds exclusively on nectar.—b. *Desmodus rotundus* feeds principally on blood.

sonal communication). It seems therefore that this phenomenal adaptation of the Neem Tree to the Accra Plains may eventually result in partial or total elimination of the native flora and fauna.

GENERAL REMARKS

Plant and bat interaction on the Accra Plains offers an ideal situation for an intensive, quantitative study of this coastal-savannah ecosystem. The rate at which the original vegetation is being altered is certainly alarming, especially if we consider that it was only sixty years ago that *Azadirachta indica* was introduced to West Africa. The rapid adaptation of neem fruit as one of the major food sources of West African fruit bats is spectacular, and during the past five years population growth of fruit bats has seemed phenomenal.

It is of crucial importance that we understand the impact of the rapidly changing vegetation of the Accra Plains on the faunal elements native to this region. In addition, a systematic monitoring of what may eventually be an extreme population congestion of fruit bats in southeastern Ghana must be undertaken. Few quantitative data exist as to the influence West African fruit bats have on health and human welfare. It is therefore necessary that we amass all the information we can obtain from their activities in this region.

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